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## Effects of competition and phosphorus fertilization on leaf and root traits of late-successional conifers *Abies fabri* and *Picea brachytyla*

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3 Effects of competition and phosphorus fertilization on leaf and root traits of  
4 late-successional conifers *Abies fabri* and *Picea brachytyla*

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21  
22 **Head title:** Phosphorus effect on functional traits of plants

1   **Abstract** Leaf and root systems are known to show a high degree of developmental  
2   plasticity in response to the local environment. However, few studies have investigated  
3   simultaneously the leaf and root traits as affected by competition and phosphorus (P)  
4   fertilization, especially in connection with the primary succession. We investigated  
5   morphological and physiological responses to different competition treatments (intra- vs.  
6   interspecific competition) and P regimes in seedlings of *Abies fabri* and *Picea brachytyla*,  
7   collected from the late succession stage Hailuoguo glacier retreat area. *A. fabri* had a  
8   greater total chlorophyll content and specific leaf area (SLA), higher leaf nitrogen (N)  
9   and P concentrations, as well as a higher water use efficiency (assessed by the carbon  
10   isotope composition,  $\delta^{13}\text{C}$ ) and N absorption relative to *P. brachytyla* under P fertilization  
11   conditions, and its total biomass responded more strongly to P fertilization, especially  
12   under interspecific competition. P fertilization decreased the specific root length (SRL)  
13   and ectomycorrhizal infection in both species and specific root tip density in *P.*  
14   *brachytyla* but it had no effect on the average root diameter. We concluded that similar  
15   changes in root characteristics, but the superior performance of above-ground traits in *A.*  
16   *fabri* in response to P availability, especially under competition, explain the greater  
17   competitive capacity of *A. fabri* at final stages of succession. These findings highlight the  
18   influence of soil nutrition availability and competition on the functional traits of plants  
19   and contribute to the understanding of the role of relative modifications in leaf and root  
20   traits during succession.

21   **Keywords:** competition; soil P availability; plant functional traits; trait correlations;  
22   primary succession

## 1. Introduction

Plants are exposed to multiple stresses, including both biotic (e.g. competition) and abiotic factors (e.g. soil nutrient availability). Competition is a major biotic factor that affects plant survival and growth, species abundance and distribution, and the composition of plant communities (Williams and McCarthy, 2001; Michalet, 2006). Competition is a complex stress that affects plants' aerial and belowground environment. Previous studies have indicated that it can lead to morphological responses and changes in resource allocation (Novoplansky, 2009; Yamawo, 2015), photosynthetic capacity (Poorter et al., 2012; Duan et al., 2014), water use efficiency ( $\delta^{13}\text{C}$ ) (Duan et al., 2014), nitrogen (Miller et al., 2007; Ashton et al., 2008) and phosphorus (Müller and Bartelheimer, 2013) absorption, and non-structural carbohydrate metabolism (Guo et al., 2016). Such structural, physiological and chemical modifications ultimately affect plants' performance and competitive status in different environments.

Competition often interacts with abiotic stresses, resource availability and environmental heterogeneity at different time scales (Sardans et al., 2004; Niinemets, 2010a; Chen et al., 2014; Duan et al., 2014; Guo et al., 2016). Phosphorus (P) is a key abiotic resource that affects plants at the biochemical and ecophysiological levels by directly influencing metabolic processes but also by altering competitive interactions in the ecosystem (Williamson et al., 2001; Sterner and Elser, 2002; Vance et al., 2003; Turnbull et al., 2007; Yu et al., 2017). P is usually the most limiting element in terrestrial ecosystems (Elser et

1 al., 2007; Vitousek et al., 2010), especially during the later stages of succession when  
2 much of the soil phosphorus may be present in standing biomass, plant litter and  
3 organic soil matter in forms unavailable to plants (Brais et al., 1995; Holdaway et al.,  
4 2011). Variation in soil P availability can influence individual competitiveness, species  
5 diversity, and the structure, functioning and dynamics of ecosystems (Williamson et al.,  
6 2001; Reich and Oleksyn, 2004; Lambers et al., 2011). There are several strategies for  
7 plants to avoid or cope with resource (e.g. P) limitations, including altered biomass  
8 allocation (Shipley and Meziane, 2002; Poorter et al., 2012), morphological or  
9 physiological adaptation of growth or developmental processes (plasticity) (Gedroc et al.,  
10 1996; Aphalo et al., 1999; Callaway et al., 2003), tolerance (Grime, 1979), and resource  
11 investments into endo- and ectomycorrhizal associations to increase nutrient uptake  
12 (Chiariello et al., 1982; Smith et al., 1999; Tuomi et al., 2001).

13

14 Plants can adjust the share of biomass allocation between roots and shoots depending on  
15 whether the most limiting resource conditions occur above- or belowground (Shipley and  
16 Meziane, 2002; Poorter et al., 2012). For example, plants can modify biomass allocation  
17 and invest relatively more into roots under water- or nutrient-limited conditions (Dong et  
18 al., 2016; Song et al., 2017). As a response to abiotic stresses, plants can also adjust their  
19 morphology to increase the uptake of most limiting resources (Ryser and Eek, 2000; Hill  
20 et al., 2006; Niinemets, 2010b) to the extent that these adjustments that enhance the  
21 efficiency of uptake of resources might be more important than changes in the total mass  
22 allocation (Poorter et al., 2012). Commonly, a decreasing light availability causes an

1 increase in the leaf area per unit mass (specific leaf area, SLA; Rijkers et al., 2000; Evans  
2 and Poorter, 2001; Niinemets et al., 2015). Belowground, an increasing nutrient  
3 limitation is generally associated with an increasing specific root length (SRL) (Hill et al.,  
4 2006; Ostonen et al., 2007), which represents the length of roots potentially able to  
5 explore soil per unit mass invested. In addition to morphological plasticity, endo- and  
6 ectomycorrhizal associations play important roles in the growth and establishment of  
7 seedlings (Chiariello et al., 1982; Smith and Read, 1997). Endo- and ectomycorrhizal  
8 associations are especially important for nutrient mobilization and uptake by plants in  
9 nutrient limited environments (Chiariello et al., 1982; Smith and Read, 1997), e.g. in  
10 conditions encountered in late-successional stages of ecosystems, where P is often the  
11 main limiting nutrient (Brais et al., 1995; Holdaway et al., 2011). To gain an insight into  
12 changes in species competitiveness during succession, it is also important to examine  
13 variation in leaf and root traits among different competition patterns, and to determine  
14 how they change along environmental gradients (e.g. Craine et al., 2005; Liu et al., 2010),  
15 particularly depending on the availability of soil nutrients (Coomes and Grubb, 2000;  
16 Lambers et al., 2008).

17

18 Across habitats, plants may experience selection pressures with varying severity (Price et  
19 al., 2014), and correlated variation patterns among leaf and root traits have been observed  
20 (Craine and Lee, 2003; Liu et al., 2010; Holdaway et al., 2011). For example, leaf and  
21 root N (Craine and Lee, 2003; Craine et al., 2005; Tjoelker et al., 2005; Freschet et al.,  
22 2010; Liu et al., 2010) and P concentrations (Kerkhoff et al., 2006; Newman and Hart,

1 2006; Holdaway et al., 2011) have consistently been found to be positively correlated.  
2 However, the relationships among key above- and belowground morphological traits  
3 (SLA and SRL), which represent plants' resource acquisition strategies (Wright et al.,  
4 2004; Li and Bao, 2015; Cheng et al., 2016), are poorly understood, and the results  
5 obtained so far are fragmented and inconsistent. For instance, positive correlations  
6 between SLA and SRL have been found among temperate trees in central Poland  
7 (Withington et al., 2006), while Tjoelker et al. (2005) detected no relationship between  
8 SLA and SRL in 39 grassland and savanna species. Holdaway et al. (2011) discovered  
9 that along a soil chronosequence, there was a weak positive correlation between SLA and  
10 SRL, but this relationship became obscure when SRL increased and SLA declined with  
11 an increasing site age. However, only few studies have investigated how morphological  
12 traits are influenced by interactions with neighbors and how the relationship between  
13 SLA and SRL is altered by changes in P availability during primary succession, e.g., in  
14 glacier retreat areas, where profound changes occur in vegetation composition depending  
15 on the age of the glacier meltdown (Lei et al., 2015; Song et al., 2017).

16

17 The Hailuoguo glacier retreat area in the Gongga Mountain region (Southwest China),  
18 has a characteristic primary succession series, including N-fixing species dominating the  
19 most recent meltdown areas, followed by deciduous shrubs of *Salix* and *Populus*, and the  
20 climax community, which is dominated by *Abies fabri* and *Picea brachytyla* (Luo et al.,  
21 2012; Zhou et al., 2013; Lei et al., 2015). Among the late successional conifer species, *A.*  
22 *fabri* appears during later stages of succession, followed by *P. brachytyla* as a

1 co-dominant species (Zhou et al., 2013; Lei et al., 2015). *A. fabri* and *P. brachytyla* occur  
2 mainly in the mountainous regions of Western Sichuan, China. They are endemic and  
3 dominant species of the subalpine dark coniferous forests (Wu, 1995; Liu, 2002; Guo et  
4 al., 2010). During the primary succession, soil nutrient availability changes from the  
5 initial N limitation of primary production to P limitation (Walker and Syers, 1976;  
6 Vitousek et al., 2010; Lei et al., 2015; Song et al., 2017). The responses of leaf and root  
7 traits to successional variation in soil nutrient (e.g. P) availability have important  
8 implications for understanding the drivers of vegetation changes during the primary  
9 succession.

10  
11 In this study, we explored how the biotic factor (competition) and the abiotic factor (soil  
12 P availability) alone and in combination affect leaf and root traits in *A. fabri* and *P.*  
13 *brachytyla*. We quantified variation in root traits (SRL, average root diameter, specific  
14 root tip density, nutrient and non-structural carbohydrate contents, ectomycorrhizal  
15 associations) and the relationships among root and leaf traits (SLA, net photosynthetic  
16 rate, nutrient and non-structural carbohydrate contents) in *A. fabri* and *P. brachytyla*  
17 across competition and P fertilization treatments in the Hailuoguo glacier retreat area. In  
18 addition, different forms of  $^{15}\text{N}$ -labeled nitrogen sources ( $^{15}\text{NH}_4\text{NO}_3$  and  $\text{NH}_4^{15}\text{NO}_3$ )  
19 were utilized to determine, whether *A. fabri* and *P. brachytyla* exhibit differentiation in  
20 absorbing nitrogen under different treatments. The following hypotheses were tested: (1)  
21 competition and P fertilization alter both morphological and physiological traits of *A.*  
22 *fabri* and *P. brachytyla*, and, consequently, influence the competitiveness of these two



1 conifers, (2) *A. fabri* has superior growth characteristics due to more efficient above- and  
2 belowground resource harvesting under P fertilization and competition, and (3) the  
3 relationships among leaf and root traits in these two conifers are influenced by soil P  
4 availability and competition, providing further insight into changes in species  
5 competitiveness during succession.

## 2. Materials and methods

### 2.1. Study site, plant material and experimental design

Our study was conducted at the Gongga Mountain Alpine Ecosystem Observation and Experiment Station of the Chinese Academy of Sciences located at the south-eastern fringe of the Tibetan Plateau (29°34' N, 101°59' E, 3000 m above sea level), where the mean annual temperature, annual precipitation and relative humidity are 4.2 °C, 1947 mm and 90.2% (averages over 22 years; Yu et al., 2017). The Hailuoguo glacier retreat area is 2 km away from the station and the climatic conditions are similar.

Healthy *A. fabri* and *P. brachytyla* seedlings with a height of about 25 cm were selected from a nursery near the station. Two seedlings (10 cm apart from each other) were planted in each plastic pot (external diameter 32 cm, height 25 cm) with native soil in mid-September 2014. The planting soil was obtained from the natural habitat dominated by *P. brachytyla* and had a pH of  $5.33 \pm 0.03$ , soil organic matter content of  $79.56 \pm 6.66$  g kg<sup>-1</sup>, total N content of  $1.36 \pm 0.04$  g kg<sup>-1</sup>, and total P content of  $0.57 \pm 0.03$  g kg<sup>-1</sup>.

The competition treatments were designed as follows: monoculture planting (Mon) of *A. fabri* + *A. fabri* and *P. brachytyla* + *P. brachytyla* (intraspecific competition) and mixed planting (Mix) of *A. fabri* + *P. brachytyla* (interspecific competition). Mon+P and Mix+P were monoculture planting with P fertilization and mixed planting with P fertilization,

1 respectively. The experimental layout was completely randomized with three factors  
2 (species, competition, and P fertilization). Twenty replicates per treatment were included  
3 in the experiment. The experiment was performed in an open area under rain-fed  
4 conditions. P fertilization was provided as  $\text{NaH}_2\text{PO}_4$ , 0.4 g P per pot in P-fertilized  
5 treatments (see, Siddique et al., 2010; Chen et al., 2015). Plants were watered every other  
6 day. The seedlings were fertilized on 6 May 2015 and harvested in late August 2016. In  
7 addition, in the  $^{15}\text{N}$  tracer experiment, labeled  $^{15}\text{NH}_4\text{NO}_3$  and  $\text{NH}_4^{15}\text{NO}_3$  solutions were  
8 injected into the soil at the depth of 5 cm around the rhizosphere (30 mg per plant) in all  
9 treatments (five replicates in each case). 72 h after the application of  $^{15}\text{N}$  solution, the  
10 plants were harvested and  $^{15}\text{N}$  values of leaves were determined.

11

## 12 *2.2. Analyses of plant morphology, biomass and ectomycorrhizal infection*

13

14 At the end of the experiment, five plants from each treatment were selected randomly for  
15 biomass measurements. The selected plants were harvested and divided into leaves, stems,  
16 fine roots (<2 mm in diameter) and coarse roots (>2 mm in diameter). The dry mass of all  
17 biomass samples was determined after oven-drying at 70 °C to a constant mass. The  
18 root/shoot ratio (R/S ratio) was calculated as follows: total root biomass / (leaf biomass +  
19 stem biomass). Current-year leaves were scanned and the leaf area was estimated by  
20 ImageJ software (National Institutes of Health, Bethesda, MD, USA). The specific leaf  
21 area (SLA, leaf area per unit dry mass) for current-year leaves was calculated as the ratio  
22 of the projected leaf area to leaf dry mass. Root samples were analyzed by WinRHIZO

1 root-scanning software (Regent Instruments Inc., Ottawa, ON Canada). Specific root  
2 length (SRL) was calculated for selected root samples as the ratio of the length of roots to  
3 their dry mass (Wang et al., 2006; Dong et al., 2016). Specific root tip density (SRD) was  
4 calculated as the ratio of root tip to root length, and the average root diameter (AD) was  
5 also measured (Guo et al., 2016). The rate of ectomycorrhizal infection (ECM) was  
6 analyzed by counting the total number of mycorrhizal tips per seedling and by calculating  
7 the extent of the infection as the percentage of root tips that were mycorrhizal (Dehlin et  
8 al., 2004; Yin et al., 2013).

9

### 10 *2.3. Determination of leaf gas exchange characteristics and chlorophyll content*

11

12 The light-saturated net photosynthetic rate ( $P_n$ ) was measured with a LI-COR 6400  
13 portable photosynthesis system (LI-COR, Lincoln, NE, USA) with a conifer chamber  
14 (PLC-broad, PP Systems) for intact current-year leaves in five randomly chosen  
15 individuals in each treatment between 08:00 and 11:30 at the end of July 2016. The  
16 standard measurement conditions were as follows: leaf temperature, 25 °C; water vapor  
17 pressure deficit,  $1.5 \pm 0.5$  kPa (corresponding to relative humidity of 50%); light intensity  
18 (PPFD),  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; and  $\text{CO}_2$  concentration,  $400 \pm 5 \mu\text{mol mol}^{-1}$ . Once the  
19 steady-state gas exchange rates were observed, the light-saturated net photosynthetic rate  
20 ( $P_n$ ) was recorded.

21

22 In addition to leaves used in photosynthesis measurements, additional neighboring leaves

1 were randomly sampled for chlorophyll content measurements. The chlorophyll content  
2 was determined by spectrophotometry according to the method of Lichtenthaler (1987)  
3 using a UV-330 spectrophotometer (Unicam, Cambridge, UK). The total chlorophyll  
4 content (*TChl*) was calculated as the sum of chlorophyll *a* and *b*.

#### 6 *2.4. Determination of N and P contents*

8 For both N and P analyses, 0.2 g of dry powdered material was used. The N content was  
9 determined by a semi-micro Kjeldahl method (Mitchell, 1998), and the P content by  
10 induced plasma emission spectroscopy (Hötscher and Hay, 1997).

#### 12 *2.5. Determination of non-structural carbohydrates*

14 Leaf and root samples from five randomly chosen individuals in each treatment were  
15 collected for non-structural carbohydrate analyses at the end of the experiment. Total  
16 soluble sugar and starch contents were determined as glucose equivalents by the anthrone  
17 method according to Yemm and Willis (1954). Methodological details of these  
18 measurements have been described by Guo et al. (2016) and Yu et al. (2017).

#### 20 *2.6. Determination of carbon and nitrogen isotope composition*

22 The stable isotope analyses were conducted at the Stable Isotope Laboratory for

1 Ecological and Environmental Research, Chinese Academy of Forestry using a DELTA V  
2 Advantage Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Inc., Waltham,  
3 MA, USA). The carbon isotope composition ( $\delta^{13}\text{C}$ ) was determined for the same leaves,  
4 which had been used for  $P_n$  estimation. Each leaf sample was dried at 70 °C until  
5 constant mass. Dried leaves were ground, and  $^{13}\text{C}/^{12}\text{C}$  ratios were determined with an  
6 isotope ratio mass spectrometer (Thermo Fisher Scientific, Inc., USA). The carbon  
7 isotope composition was expressed as  $\delta^{13}\text{C}$  values, relative to the standard Pee Dee  
8 Belemnite (Farquhar et al., 1989) as follows:  $\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$ , where  
9  $R_{\text{sample}}$  is the  $^{13}\text{C}/^{12}\text{C}$  ratio of the sample and  $R_{\text{standard}}$  that of the standard.

10

11 In the  $^{15}\text{N}$  tracer experiment, fully-expanded intact mature leaves from the same upper  
12 position of the cuttings were sampled in each treatment 72 h after the application of  $^{15}\text{N}$ .  
13  $^{15}\text{N}/^{14}\text{N}$  ratios were determined, and the N isotope composition was expressed as  $\delta^{15}\text{N}$ .  
14 The overall precision of the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  estimations was better than 0.1‰, as  
15 determined from repetitive samples in each case.

16

## 17 2.7. Statistical analyses

18

19 Individual traits among treatments were compared by Tukey's test after one-way  
20 ANOVAs. Three-way ANOVAs were employed to test the effects of species, competition,  
21 phosphorus and their interactions. All statistical effects were considered significant at  $P <$   
22 0.05. Partial correlations were used to exclude the possibility that correlations between

1 leaf and root traits were due to the impact of competition or P fertilization, or both.  
2 Before analyses, data were checked for normality and the homogeneity of variances and  
3 log-transformed to correct for deviations from these assumptions when needed. All  
4 analyses were carried out using the Statistical Package for the Social Sciences (SPSS,  
5 Chicago, IL, USA) version 18.0.

### 3. Results

#### 3.1. Differences in plant morphology, biomass and allocation

Under P fertilization, significantly greater organ (leaf, stem and root) and total biomass were detected in *A. fabri* under interspecific competition compared to intraspecific competition, while *P. brachytyla* showed no differences between the two competition treatments. Interactive effects of competition  $\times$  P fertilization and species  $\times$  competition  $\times$  P fertilization on organ (leaf, stem and root) and total biomass (Figure 1a-e) were discovered. Thus, the interspecific competition significantly promoted the growth of *A. fabri* under P fertilization. In addition, the R/S ratio of *A. fabri* decreased under P fertilization, but the R/S ratio of *P. brachytyla* did not vary significantly among treatments, again implying a significant species  $\times$  P fertilization interaction (Figure 1f).

P fertilization decreased SRL and ECM of both species and SRD of *P. brachytyla*, while AD showed no significant differences between competition treatments and tended to increase in response to P fertilization (the P fertilization effect alone was significant for all four root traits, Figure 2). Interspecific competition promoted SRL of both species, especially when without P fertilization (Figure 2a). In addition, the interaction of species  $\times$  competition  $\times$  P fertilization significantly affected SRL, and the combination of P fertilization and interspecific competition slightly increased SRL of *A. fabri*. The interaction of competition  $\times$  P fertilization significantly influenced ECM; under P



fertilization, the reduction in ECM was stronger under interspecific competition.

### 3.2. Differences in leaf gas exchange and $\delta^{13}\text{C}$

Under P fertilization,  $P_n$ ,  $TChl$  and SLA of both species increased, and *A. fabri* had the greatest values of  $P_n$ ,  $\delta^{13}\text{C}$ ,  $TChl$  and SLA under interspecific competition (Figure 3a-d). The interaction of species  $\times$  competition, and competition  $\times$  P fertilization significantly affected  $P_n$  and  $TChl$ , and the interaction of species  $\times$  competition  $\times$  P fertilization significantly influenced  $\delta^{13}\text{C}$  and SLA.

### 3.3. Differences in concentrations of N, P and non-structural carbohydrates

Under P fertilization, interspecific competition significantly increased the leaf N concentration (LNC) of *A. fabri* but decreased it in *P. brachytyla*, whereas the root N concentration (RNC) showed a contrasting pattern (Figure 4a, b). P fertilization significantly increased leaf and root P concentrations (LPC and RPC) in both species under both intraspecific or interspecific competition, and *A. fabri* had the highest leaf and root P concentrations under interspecific competition (Figure 4c, d). In addition, the interactions of competition  $\times$  P fertilization and species  $\times$  competition  $\times$  P fertilization significantly influenced leaf and root N and P concentrations.

Leaf NSC concentrations of both species tended to decrease by P fertilization, except for

1 leaf NSC in *P. brachytyla* under intraspecific competition (Figure 4e). In addition,  
2 interspecific competition reduced leaf NSC concentrations (Figure 4e). Root NSC  
3 concentrations of both species significantly increased by P fertilization (Figure 4f).  
4 Furthermore, *A. fabri* subjected to interspecific competition with P fertilization had a  
5 higher root NSC concentration compared to intraspecific competition, while *P. brachytyla*  
6 showed no differences between the two competition treatments (Figure 4f).

#### 8 3.4. Differences in $\delta^{15}\text{NH}_4^+\text{-N}$ and $\delta^{15}\text{NO}_3^-\text{-N}$

9  
10 P fertilization significantly decreased  $\delta^{15}\text{NH}_4^+\text{-N}$  of both species under interspecific  
11 competition compared to intraspecific competition (Figure 5a). In addition, under P  
12 fertilization, both species had greater  $\delta^{15}\text{NO}_3^-\text{-N}$  under interspecific competition  
13 compared to intraspecific competition, and *A. fabri* showed highest  $\delta^{15}\text{NO}_3^-\text{-N}$  under  
14 interspecific competition and P fertilization treatment (Figure 5b).

#### 16 3.5. Relationships among leaf and root traits

17  
18 When partial correlations were used to statistically remove the influence of P fertilization  
19 or both competition and P fertilization, SLA was positively correlated with SRL (Table 1a,  
20 b). However, without correcting for the influence of both competition and P fertilization  
21 or the influence of competition, SLA was negatively correlated with SRL (Table 1a, b). In  
22 addition, LPC was positively correlated with RPC,  $P_n$ ,  $\delta^{13}\text{C}$ , *TChl*, SLA and  $\delta^{15}\text{NO}_3^-\text{-N}$ ,

- 1 and LNSC was negatively correlated with RNSC both with or without the statistical
- 2 influence of competition or P fertilization, or their combination (Table 1a, b).

## 4. Discussion

### 4.1. Changes in biomass and allocation, and in morphological traits in response to competition and P fertilization treatments

Our results showed that biomass accumulation and allocation (including leaves, stems, fine roots and total biomass, and R/S ratio; Figure 1) as well as morphological traits (SRL, AD, SRD and SLA; Figures 2a-c, 3d) of *A. fabri* and *P. brachytyla* were significantly affected by competition and P fertilization, as previously observed in several coniferous species (Dehlin et al., 2004; Duan et al., 2014). In particular, in the control treatment (no P fertilization), there were no differences in the total biomass of either species between intra- and interspecific competition (Mon versus Mix) (Figure 1d). Under P fertilization, *A. fabri* had a higher total biomass under interspecific competition than under intraspecific competition, but *P. brachytyla* showed no differences between the two competition treatments (Mon+P versus Mix+P) (Figure 1d). These findings indicated that interspecific competition significantly promoted the growth of *A. fabri*, which was the species responding more strongly to P fertilization. This can be a key factor allowing more shade tolerant *A. fabri* to gain a competitive advantage over *P. brachytyla* in closed stands in climax communities. In addition, P fertilization significantly decreased the R/S ratio of *A. fabri*, thus indicating that this species has more plasticity in its biomass allocation in response to environmental conditions, confirming previous observations (Guo et al., 2016; Song et al., 2017). Such plasticity is relevant, as investing relatively

1 more into roots under nutrient-limited conditions allows for a more efficient capture of  
2 limiting soil nutrients, especially less movable nutrients, such as P (Shipley and Meziane,  
3 2002; Portsmouth and Niinemets, 2007).

4

5 Under P fertilization, *A. fabri* had higher SLA under interspecific competition than under  
6 intraspecific competition, but SLA of *P. brachytyla* showed no differences between the  
7 two competition treatments (Mon+P versus Mix+P) (Figure 3d). Species with high SLA  
8 are generally associated with high growth rates and superior above-ground resource  
9 acquisition ability in resource-rich conditions (Reich et al., 1999; Westoby et al., 2002).

10 The higher growth rate (Yu et al., 2017) and SLA of *A. fabri* observed under interspecific  
11 competition and P fertilization (Mix+P) are in line with these previous observations.

12 Earlier studies have shown that SRL is positively related to the water and nutrient uptake  
13 capacity of roots (Eissenstat, 1991; Pregitzer et al., 2002; Comas and Eissenstat, 2004;

14 Wang et al., 2006). We found that P fertilization significantly decreased SRL and SRD of  
15 both species (Figure 2a, c); similarly Ostonen et al. (2007) and Fan et al. (2015) have

16 observed that fertilization significantly decreases SRL. A possible explanation for a  
17 decrease in SRL in response to fertilization is that under improved nutrient availability

18 less fine roots are needed to support the growth of aboveground plant parts. Thus, a  
19 functional balance between above- and belowground plant parts is achieved at a lower

20 R/S ratio under fertilization (Figure 1f). However, there was no significant increase in AD  
21 in either species under P fertilization (Figure 2b). This result is in good agreement with

22 Eissenstat et al. (2000), who reported that the fine-root diameter of tree species varied

only little along gradients of soil fertility and was unresponsive or minimally responsive to fertilization (Tingey et al., 1997; Ostonen et al., 2007; Wurzbürger and Wright, 2015).

In addition to modifications in the morphological traits of roots, the level of ectomycorrhizal infection of both species significantly decreased under P fertilization (Figure 2d), as has also been shown in a previous meta-analysis, which highlighted that P fertilization reduced mycorrhizal colonization across many ecosystem types (Treseder, 2004). In our study, we discovered strong interactions among species  $\times$  competition  $\times$  P fertilization for SLA and SRL (Figures 2a, 3d), as under P fertilization, SLA and SRL of *A. fabri* increased under interspecific competition. Such interactions showed that species-specific responses in these traits increase along environmental gradients; also implying contrasting life history strategies in the two studied species under different ecological scenarios. Thus, our findings provide important insights into predicting the potential responses of different conifer species to soil nutrient availability along successional gradients.

#### *4.2. The effects of competition and P fertilization on leaf photosynthetic capacity and chlorophyll content, and leaf and root N, P and non-structural carbohydrate contents*

N is the necessary component of proteins, nucleic acids, chlorophylls and many secondary metabolites of plants (Luo et al., 2013), while P is involved in cellular energy transfer (Marschner, 1995) and it is a vital constituent of numerous plant metabolites,

1 including nucleic acids, sugar esters and phosphorylated lipids (Niinemets and Kull, 2005;  
2 Gan et al., 2015). Therefore, strong positive relationships between photosynthetic  
3 capacity and leaf N and P concentrations are frequently observed (Evans, 1989; Wright et  
4 al., 2004; Hidaka and Kitayama, 2009). The present study indicated that *A. fabri* has a  
5 higher net photosynthetic rate ( $P_n$ ), total chlorophyll concentration (*TChl*), and leaf N and  
6 P concentrations compared to *P. brachytyla* under interspecific competition and P  
7 fertilization (Mix+P) (Figures 3a, b, 4a, c). The superior photosynthetic performance of *A.*  
8 *fabri* under interspecific competition and P fertilization conditions was associated with a  
9 greater N and P acquisition capacity as well as a higher leaf *TChl* concentration (Figure  
10 3b). In addition, these traits were associated with a higher long-term water use efficiency  
11 in *A. fabri* than in *P. brachytyla* under interspecific competition and P fertilization  
12 (Mix+P) (Figure 3c; see Farquhar et al., 1989 and Livingston et al., 1999 for discussion  
13 of the interpretation of stable carbon isotope composition values). Thus, all this evidence  
14 indicates that the performance of *A. fabri* is favored under interspecific competition.  
15 Apart from the root traits affected by P fertilization, the greater competitive capacity of *A.*  
16 *fabri* under interspecific competition might be associated with its greater shade tolerance.  
17 As aboveground biomass, especially leaf biomass, increases upon P fertilization (Figure  
18 1a, b), the performance of a species with greater shade tolerance is expected to be  
19 enhanced more strongly (Valladares and Niinemets, 2008; Valladares et al., 2016).  
20  
21 Non-structural carbohydrates (NSC) are important products of photosynthesis and they  
22 play crucial roles as plant signaling molecules in gene transcription, and also serve as a

1 storage of energy for growth and respiration as well as a carbon source for growth. NSC  
2 concentrations can be used as indicators of the balance between C supply  
3 (photosynthesis), C demand (respiration) and C storage (Chapin et al., 1990; Stitt and  
4 Schulze, 1994; Secchi and Zwieniecki, 2011; Sala et al., 2012; Wiley et al., 2013). In this  
5 study, we found that *A. fabri* had higher root NSC concentrations under interspecific  
6 competition in both non-fertilized and P-fertilized plants compared to intraspecific  
7 competition, while *P. brachytyla* showed no differences between the two competition  
8 treatments (Figure 4f). It has been reported that high root NSC could provide assimilation  
9 energy for nutrient uptake (Kobe et al., 2010; Pokhilko et al., 2014). Thus, an increase in  
10 the root NSC concentration might be responsible for the greater root P concentration in *A.*  
11 *fabri* under interspecific competition and P fertilization, thus providing a greater capacity  
12 for nutrient uptake, which might be a key factor responsible for the higher  
13 competitiveness of *A. fabri* subjected to interspecific competition under P fertilization.  
14 Yet, no such differences in root P concentrations were observed in non-fertilized plants,  
15 and root N concentrations were actually smaller in *A. fabri* under P fertilization and  
16 interspecific competition (Figure 4b, d), indicating that the relationship between NSC and  
17 nutrient uptake is complex.

18

#### 19 4.3. Changes in use of different nitrogen sources upon P fertilization and competition

20

21 Both species showed lower  $\delta^{15}\text{NH}_4^+\text{-N}$  and  $\delta^{15}\text{NO}_3^-\text{-N}$  under interspecific competition  
22 than under intraspecific competition, except for  $\delta^{15}\text{NH}_4^+\text{-N}$  in *P. brachytyla* (Figure 5a, b),



1 indicating that neighbors affect competition for different N sources (Miller et al., 2007;  
2 Ouyang et al., 2016; Song et al., 2017). In addition, P fertilization significantly decreased  
3  $\delta^{15}\text{NH}_4^+\text{-N}$  but increased  $\delta^{15}\text{NO}_3^-\text{-N}$  of both species under interspecific competition  
4 compared to intraspecific competition (Mon+P versus Mix+P) (Figure 5a, b). Thus, the  
5 results showed that *A. fabri* and *P. brachytyla* preferably absorb  $\text{NO}_3^-\text{-N}$  under P  
6 fertilization conditions. Ammonium is less movable in soil than nitrate and thus the lower  
7 absorption capacity for ammonium in P-fertilized plants is in accordance with the  
8 reduction in SRL, SRD and ectomycorrhizal colonization (Figure 2). Previous studies  
9 have proposed that species better adapted to more movable  $\text{NO}_3^-\text{-N}$  have a significant  
10 competitive advantage (Kronzucker et al., 1997; Song et al., 2017), as observed in *A.*  
11 *fabri* during interspecific competition under P fertilization (Figure 5b). The better  $\text{NO}_3^-\text{-N}$   
12 absorbing ability of *A. fabri* with reduced SRL, SRD and ectomycorrhizal colonization  
13 might affect its growth and physiological processes, such as assimilation and metabolism,  
14 and result in a competitive advantage under P fertilization.

15

#### 16 4.4. Competition and P fertilization alter relationships among leaf and root traits

17

18 Our study revealed a positive correlation between SLA and SRL when partial correlations  
19 were used to statistically remove the influence of P fertilization, but without removing the  
20 influence of P fertilization there was a negative correlation between SLA and SRL (Table  
21 1a, b). These results indicate that the relationship between SLA and SRL can vary  
22 depending on soil nutrient (e.g. P) availability (Wright and Westoby, 1999; Holdaway et

1 al., 2011). A likely explanation for these variable relationships is that leaf and root traits  
2 differ in their responses to soil nutrient availability (Wright and Westoby, 1999).  
3 Holdaway et al. (2011) investigated fine root traits along a 120 000-year soil  
4 chronosequence (soil P limitation increasing with soil age) in a temperate rain forest and  
5 found a weak positive correlation between SLA and SRL. They also discovered a strong  
6 positive relationship between SRL and soil age and a negative relationship between SLA  
7 and site age. These results are consistent with increasing SRL with decreasing soil  
8 nutrient availability observed by Peltzer et al. (2010) and in our study (Figure 2a).  
9 Overall, these findings highlight the importance of considering variation in soil nutrients  
10 when making generalizations about changes in root traits during succession.

11

12 In the present study, we found a significant positive relationship between leaf and root P  
13 concentrations, regardless of whether removing or not removing statistically the  
14 influences of competition or P fertilization, or both (Table 1a, b). Similarly, positive  
15 relationships between leaf and root nutrient (N and P) concentrations have been found in  
16 grassland and savannah ecosystems (Craine and Lee, 2003; Craine et al., 2005; Tjoelker  
17 et al., 2005; Liu et al., 2010), and in temperate and tropical forests (Li et al., 2010).  
18 Tjoelker et al. (2005) have suggested that a strong positive relationship in nutrient  
19 concentrations between leaves and roots reflect similar adaptations to soil nutrient  
20 limitations in aboveground and belowground plant parts. In accordance to this suggestion,  
21 positive correlations among leaf, wood, and root tissues have been observed (Ninemets,  
22 1998), indicating that the total plant nutrient pools are distributed among different plant

1 organs in a balanced manner. In our study, the significant positive relationship between  
2 leaf and root P concentrations may be due to P limitation stress during late-stage primary  
3 succession (Brais et al., 1995; Holdaway et al., 2011). On the other hand, Li and Bao  
4 (2015) have found independent variation in leaf and root N concentrations; similarly, no  
5 significant correlation between leaf and root N concentrations was observed in our study  
6 (Table 1a, b).

7

8 We observed that LPC was positively correlated with  $P_n$ ,  $\delta^{13}C$ ,  $TChl$ , SLA and  $\delta^{15}NO_3^- - N$ ,  
9 regardless of whether removing or not removing statistically the influence of competition  
10 or P fertilization, or both (Table 1a, b). Stronger relationships of physiological and  
11 structural characteristics of foliage with leaf P than with leaf N concentration have also  
12 been observed in other conifers (Reich and Schoettle, 1988). Such evidence suggests that  
13 foliage physiology is more strongly limited by P availability than N availability, as is  
14 characteristic during late stages of primary succession.

## 5. Conclusions

The present study demonstrated that competition and P fertilization affect the leaf and root traits of *A. fabri* and *P. brachytyla* and that different responses in the morphological and physiological traits between these two conifers to competition and P fertilization could be largely responsible for the competitive outcomes. *A. fabri* displayed a competitive advantage and had a greater total chlorophyll content and SLA, higher leaf N and P concentrations, as well as a higher water use efficiency ( $\delta^{13}\text{C}$ ) and N uptake ( $\delta^{15}\text{NO}_3^-$ -N) relative to *P. brachytyla* under P fertilization. In addition, the relationships between SLA and SRL changed with P fertilization, suggesting that soil nutrient availability effects on structural traits may be fundamentally different for the above- and belowground parts of plants. We suggest that further research should focus on large-scale relationships among plant traits and associated environmental factors across successional gradients.

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3

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6   Helena Korpelainen and Ülo Niinemets had a significant contribution to the interpretation  
7   of data and manuscript preparation, and Chunyang Li (the corresponding author) had the  
8   overall responsibility for experimental design and project management.

9

10   **Conflict of interest** The authors declare that they have no conflict of interest.

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**Table 1** Correlation coefficients and their significance for leaf and root traits of *Abies fabri* and *Picea brachytyla* across different P fertilization (fertilized vs. non-fertilized) and competition (intra- vs. interspecific) treatments.

	$P_n$	$TChl$	$\delta^{13}C$	SLA	SRL	ECM	$\delta^{15}NH_4^+-N$	$\delta^{15}NO_3^--N$	LNC	RNC	LPC	RPC	LNSC	RNSC
(a)														
$P_n$		0.750***	0.684***	0.692***	-0.780***	-0.805***	0.071	0.462**	0.338*	-0.458**	0.865***	0.855***	-0.298	0.769***
$TChl$	0.281		0.604***	0.892***	-0.606***	-0.845***	-0.363*	0.501***	0.445**	-0.180	0.887***	0.923***	-0.698***	0.877***
$\delta^{13}C$	0.439**	0.208		0.585***	-0.447**	-0.548***	-0.055	0.583***	0.256	-0.248	0.655***	0.646***	-0.383*	0.468**
SLA	0.033	0.372*	0.160		-0.512***	-0.734***	-0.467**	0.601***	0.692***	-0.167	0.864***	0.881***	-0.641***	0.876***
SRL	-0.185	0.100	0.098	0.555***		0.768***	-0.066	-0.336*	-0.305	0.234	-0.826***	-0.808***	0.131	-0.760***
ECM	-0.253	-0.290	-0.024	0.168	0.180		0.079	-0.331*	-0.298	0.314*	-0.891***	-0.880***	0.412*	-0.845***
$\delta^{15}NH_4^+-N$	0.495**	0.371*	0.224	-0.333*	-0.023	-0.485**		-0.294	-0.583***	-0.549***	-0.182	-0.230	0.756***	-0.335*
$\delta^{15}NO_3^--N$	0.313	0.454**	0.475**	0.589***	-0.134	0.034	-0.224		0.538***	-0.145	0.484**	0.526***	-0.470**	0.336*
LNC	-0.131	-0.037	-0.058	0.644***	0.202	0.360*	-0.726***	0.431**		-0.178	0.510***	0.513***	-0.307	0.574***
RNC	-0.494**	-0.450**	-0.200	-0.195	-0.200	0.346*	-0.536***	-0.125	-0.130		-0.300	-0.281	-0.387*	-0.165
LPC	0.398*	0.408*	0.441**	0.393*	-0.007	-0.166	0.173	0.646***	0.207	-0.496**		0.987***	-0.446**	0.926***
RPC	0.392*	0.588***	0.327*	0.383*	-0.160	-0.065	0.184	0.747***	0.188	-0.496**	0.770***		-0.510***	0.933***
LNSC	-0.009	-0.115	-0.191	-0.290	0.153	-0.168	0.347	-0.606***	-0.081	-0.509***	-0.138	-0.184		-0.514***
RNSC	-0.186	-0.088	-0.556***	0.296	0.082	0.161	0.444**	-0.166	0.444**	0.013	-0.331*	-0.162	0.042	
(b)														
$P_n$		0.846***	0.694***	0.745***	-0.799***	-0.816***	0.042	0.474**	0.347*	-0.471**	0.869***	0.870***	-0.619***	0.789***
$TChl$	0.084		0.620***	0.883***	-0.826***	-0.886***	-0.119	0.497***	0.444**	-0.386*	0.950***	0.962***	-0.713***	0.901***
$\delta^{13}C$	0.420**	0.222		0.585***	-0.500***	-0.544***	0.021	0.578***	0.248	-0.308	0.655***	0.642***	-0.542***	0.461**
SLA	-0.032	0.620***	0.199		-0.658***	-0.743***	-0.379*	0.596***	0.697***	-0.314	0.893***	0.892***	-0.733***	0.880***
SRL	-0.214	0.498***	0.149	0.691***		0.835***	0.217	-0.393*	-0.352*	0.141	-0.878***	-0.888***	0.699***	-0.853***
ECM	-0.224	-0.335*	-0.048	0.028	0.031		0.018	-0.323*	-0.291	0.377*	-0.892***	-0.879***	0.601***	-0.844***
$\delta^{15}NH_4^+-N$	0.417**	-0.422**	0.064	-0.586***	-0.425**	-0.177		-0.296	-0.738***	-0.436**	-0.218	-0.210	0.415**	-0.326*
$\delta^{15}NO_3^--N$	0.294	0.381*	0.484**	0.564***	-0.034	0.006	-0.250		0.532***	-0.208	0.483**	0.519***	-0.659***	0.323*
LNC	-0.141	0.068	-0.044	0.600***	0.230	0.327*	-0.577***	0.440**		-0.233	0.509***	0.507***	-0.401*	0.568***
RNC	-0.496***	0.050	-0.137	0.056	0.064	0.235	-0.618***	-0.062	-0.075		-0.341*	-0.353*	-0.151	-0.243
LPC	0.362*	0.414*	0.453**	0.440**	0.117	-0.203	-0.042	0.654***	0.226	-0.365*		0.990***	-0.734***	0.931***
RPC	0.290	0.694***	0.343*	0.542***	0.155	-0.153	-0.239	0.714***	0.219	-0.218	0.763***		-0.739***	0.933***
LNSC	0.096	-0.748***	-0.189	-0.594***	-0.459**	0.115	0.761***	-0.375*	-0.138	-0.545***	-0.253	-0.503***		-0.696***
RNSC	-0.215	0.359*	-0.412**	0.491***	0.347*	0.031	-0.560***	-0.072	0.438**	0.206	-0.167	0.123	-0.449**	

(a) Correlation coefficients without removing the influence of competition and P fertilization (*upper triangle*); partial correlation coefficients when removing the influence of both competition and P fertilization (*lower triangle*). (b) Partial correlation coefficients when the influence of competition was removed (*upper triangle*); partial correlation coefficients when the influence of P fertilization was removed (*lower triangle*).  $P_n$ , net photosynthetic rate;  $TChl$ , total chlorophyll content; SLA, specific leaf area; SRL, specific root length; ECM, ectomycorrhizal infection; LNC, RNC, LPC, RPC, LNSC, and RNSC indicate leaf and root N, P and NSC concentrations. \*  $0.01 < P < 0.05$ ; \*\*  $0.001 < P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ .

## Figure legends

**Figure 1.** Biomass accumulation and allocation of *A. fabri* and *P. brachytyla* under different competition treatments and P fertilization levels. (a) Leaf biomass, (b) shoot biomass, (c) total root biomass, (d) total biomass, (e) fine root biomass and (f) root/shoot ratio. Each value is the mean  $\pm$  SE of five replicate plants ( $n = 5$ ). Different lowercase letters indicate significant treatment differences among species and treatments, according to Tukey's test after one-way ANOVA at a significance level of  $P < 0.05$ . Three-way analyses of variance (ANOVA) were applied to evaluate the effects of different factors and their interactions. S, species effect; C, competition effect; P, P fertilization effect; S  $\times$  C, species  $\times$  competition effect; S  $\times$  P, species  $\times$  P fertilization effect; C  $\times$  P, competition  $\times$  P fertilization effect; S  $\times$  C  $\times$  P, species  $\times$  competition  $\times$  P fertilization effect. Black and white bars denote *A. fabri* and *P. brachytyla*, respectively. Mon: intraspecific competition; Mix: interspecific competition; Mon+P: intraspecific competition under P fertilization; Mix+P: interspecific competition under P fertilization.

**Figure 2.** (a) Specific root length (SRL), (b) average root diameter (AD), (c) specific root tip density (SRD) and (d) ectomycorrhizal infection (ECM) of *A. fabri* and *P. brachytyla* under different competition treatments and P fertilization levels. Each value is the mean  $\pm$  SE ( $n = 5$ ). Treatment codes and statistical analyses are as in Figure 1.

**Figure 3.** (a) Net photosynthetic rate ( $P_n$ ), (b) total chlorophyll concentration ( $TChl$ ), (c)

1  $\delta^{13}\text{C}$  and (d) specific leaf area (SLA) of *A. fabri* and *P. brachytyla* under different  
2 competition treatments and P fertilization levels. Each value is the mean  $\pm$  SE ( $n = 5$ ).  
3 Treatment codes and statistical analyses are as in Figure 1.

4

5 **Figure 4.** (a) Leaf N concentration, (b) root N concentration, (c) leaf P concentration, (d)  
6 root P concentration, (e) leaf NSC concentration and (f) root NSC concentration of *A.*  
7 *fabri* and *P. brachytyla* under different competition treatments and P fertilization levels.  
8 Each value is the mean  $\pm$  SE ( $n = 5$ ). Treatment codes and statistical analyses are as in  
9 Figure 1.

10

11 **Figure 5.** (a)  $\delta^{15}\text{NH}_4^+\text{-N}$  and (b)  $\delta^{15}\text{NO}_3^-\text{-N}$  of *A. fabri* and *P. brachytyla* under different  
12 competition treatments and P fertilization levels. Each value is the mean  $\pm$  SE ( $n = 5$ ).  
13 Treatment codes and statistical analyses are as in Figure 1.

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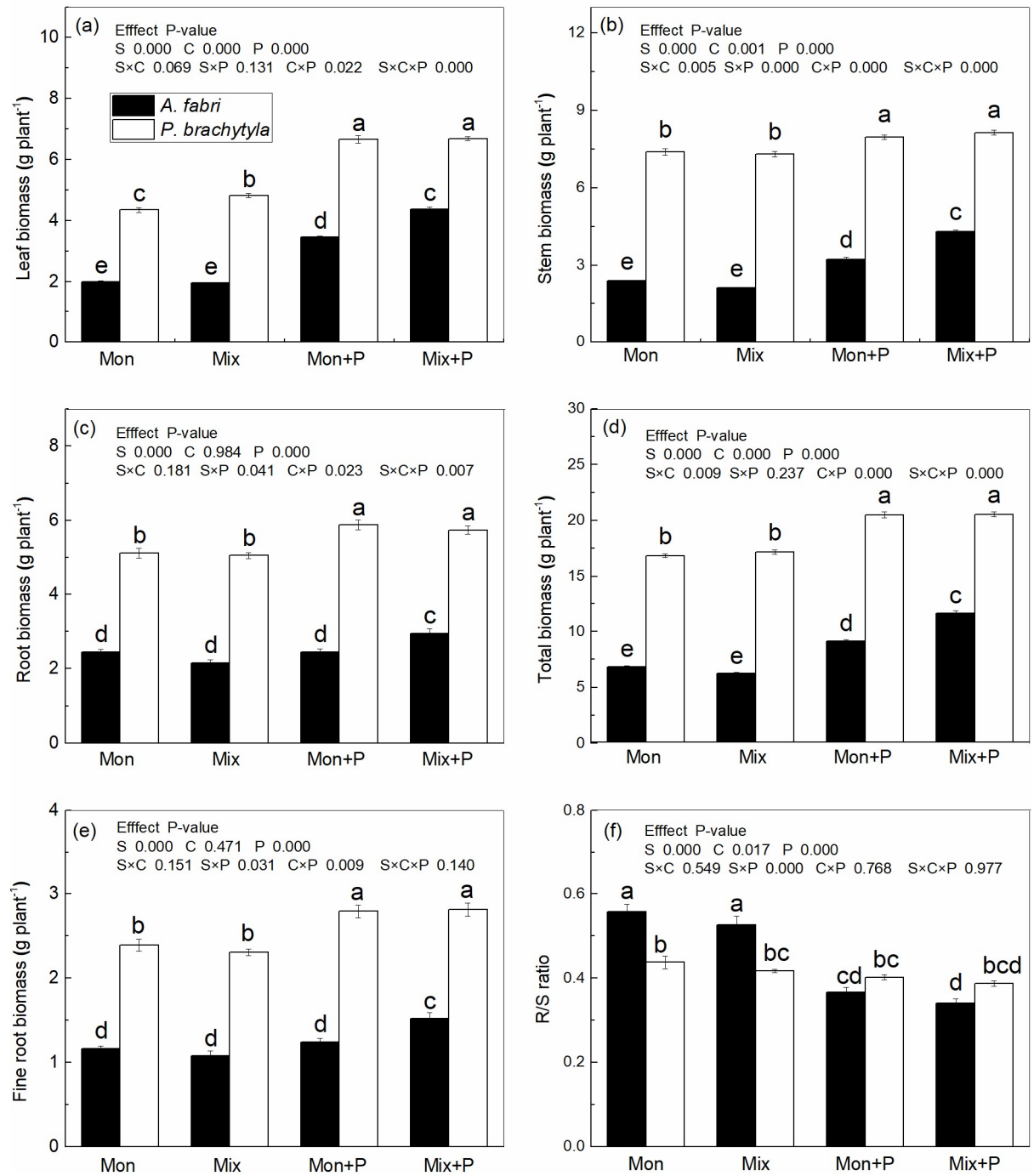
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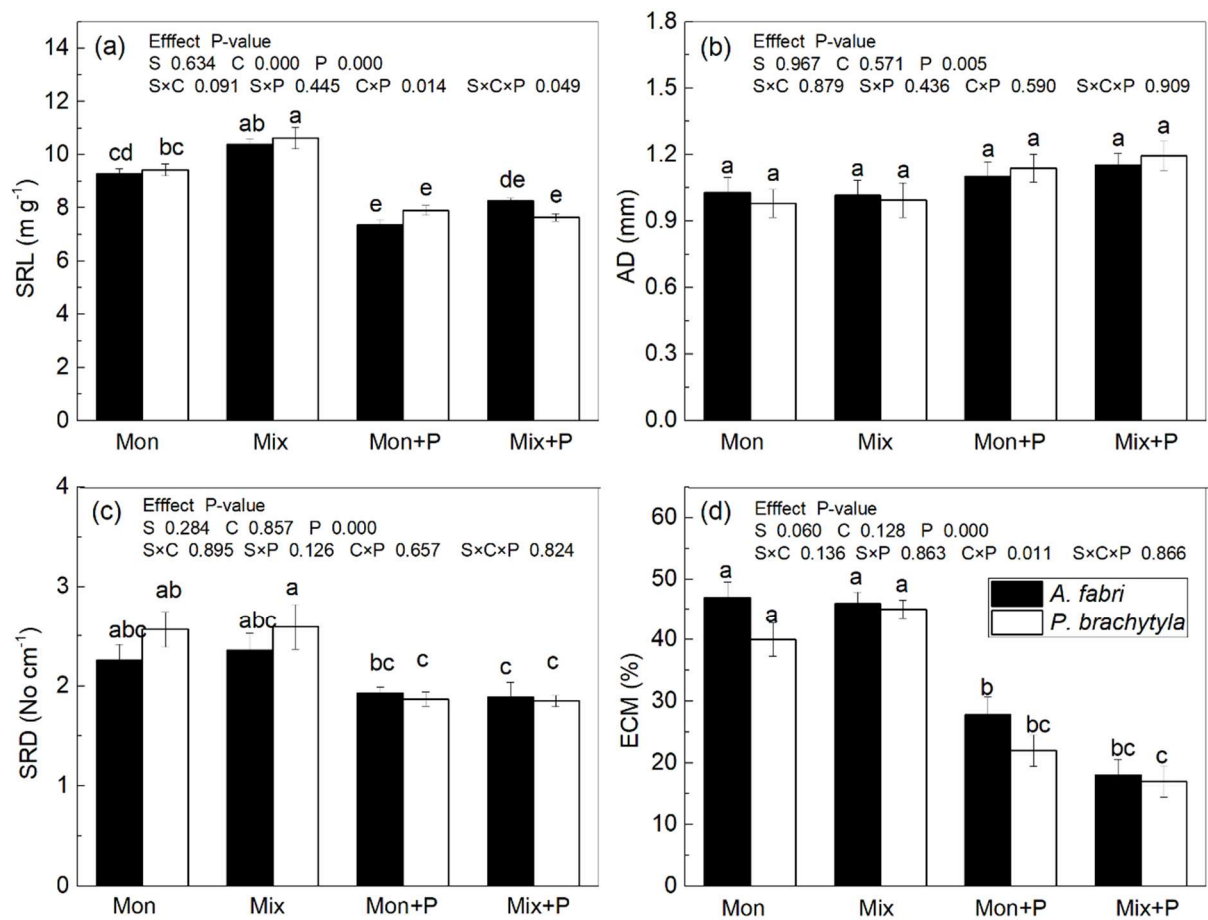
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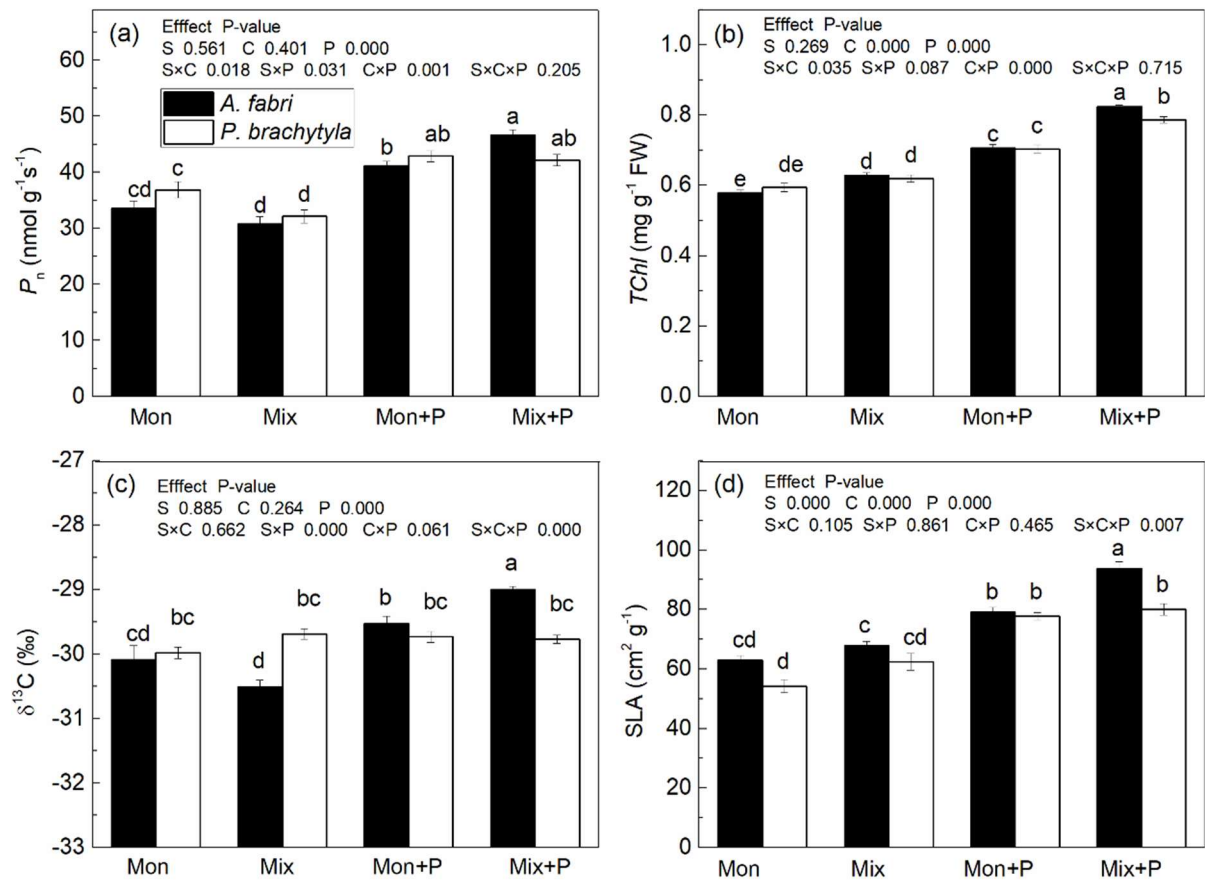
2 **Figure 1**



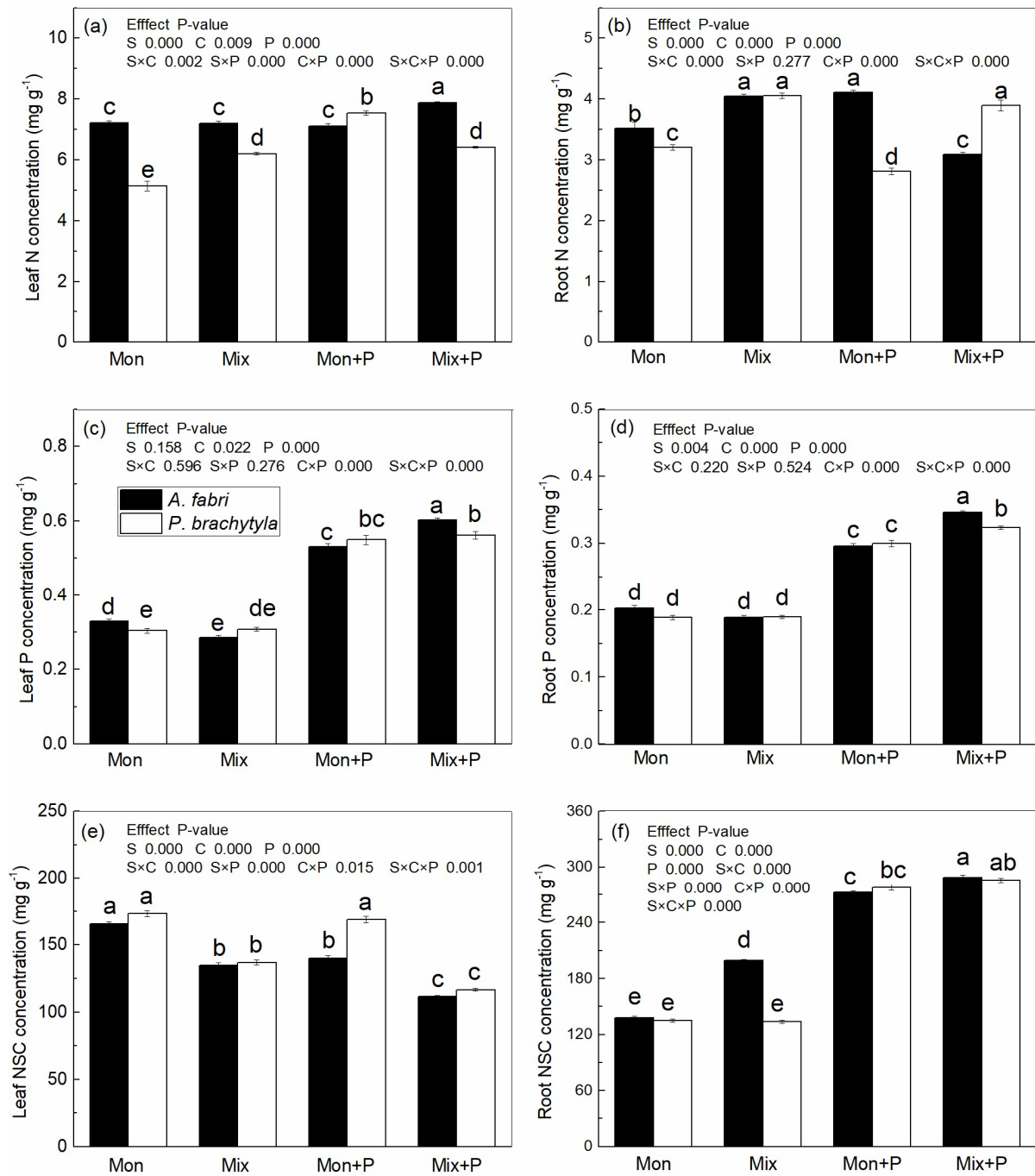
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2 **Figure 2**

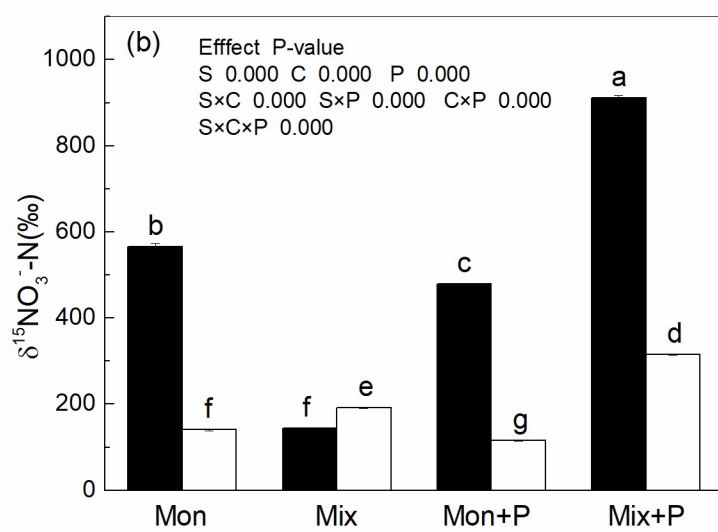
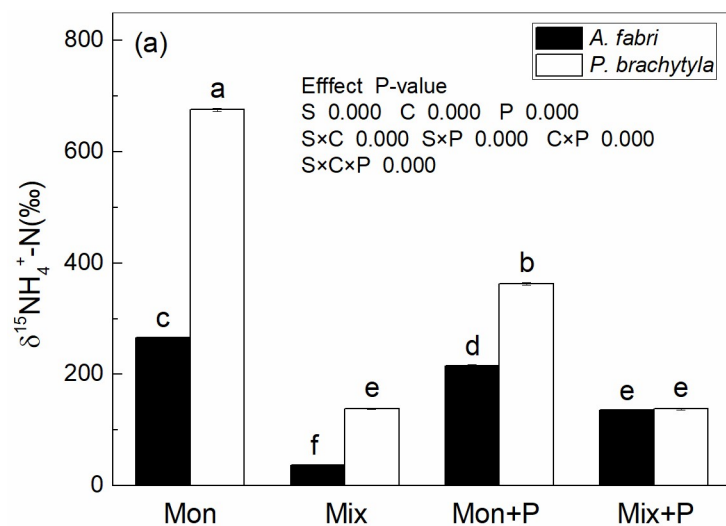




**Figure 3**



**Figure 4**



**Figure 5**